

# Adjustments and coordination of hydraulic, leaf and stem traits along a water availability gradient

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## Summary

- Trait variability in space and time allows plants to adjust to changing environmental conditions. However, we know little about how this variability is distributed and coordinated at different organizational levels.
- For six dominant tree species in northeastern Spain (three Fagaceae and three Pinaceae) we quantified the inter- and intraspecific variability of a set of traits along a water availability gradient. We measured leaf mass per area (LMA), leaf nitrogen (N) concentration, carbon isotope composition in leaves ( $\delta^{13}\text{C}$ ), stem wood density, the Huber value (Hv, the ratio of cross-sectional sapwood area to leaf area), sapwood-specific and leaf-specific stem hydraulic conductivity, vulnerability to xylem embolism ( $P_{50}$ ) and the turgor loss point ( $P_{\text{tlp}}$ ).
- Differences between families explained the largest amount of variability for most traits, although intraspecific variability was also relevant. Species occupying wetter sites showed higher N,  $P_{50}$  and  $P_{\text{tlp}}$ , and lower LMA,  $\delta^{13}\text{C}$  and Hv. However, when trait relationships with water availability were assessed within species they held only for Hv and  $P_{\text{tlp}}$ .
- Overall, our results indicate that intraspecific adjustments along the water availability gradient relied primarily on changes in resource allocation between sapwood and leaf area and in leaf water relations.

## Introduction

Understanding the patterns underlying the huge diversity in plant form and function across different organizational levels is a central goal for ecologists. This diversity arises from a combination of genetic variation and phenotypic plasticity and results in adaptations to a range of environmental conditions across space and time (Bradshaw, 1965, 2006). In recent decades, trait-based ecology has emerged as a renewed discipline with the potential to be applied to dynamic global vegetation models (Van Bodegom *et al.*, 2012; Harper *et al.*, 2016) and improve predictions of vegetation responses to environmental changes (Lavorel & Garnier, 2002; McGill *et al.*, 2006). The use of traits emphasizes species phenotypic values over taxonomic characteristics, facilitating the comparison among species and environments (Westoby & Wright, 2006). Identifying tradeoffs that appear repeatedly because of evolutionary constraints has become a major research topic because they have the potential to reflect ecological strategies (Westoby *et al.*, 2002; Laughlin, 2014; Adler *et al.*, 2014). One of the dimensions that has received more attention is the leaf economics spectrum (LES), which highlights the tradeoff between the dry mass and nutrient investments in leaf construction and the time required for obtaining returns on those

investments (Reich *et al.*, 1997; Wright *et al.*, 2004). However, how to exactly describe and integrate complex community dynamics and predict ecosystem-level responses to environmental changes from individual-level trait measurements remains a challenge (Shipley *et al.*, 2016; Funk *et al.*, 2017).

Functional variability of plants has been frequently collapsed at the species level by using mean values, thus ignoring intraspecific trait variability (ITV). However, much work has shown that ITV is relevant when making predictions about plant community assembly and ecosystem functioning (Violle *et al.*, 2012). This is particularly the case when we move from global to more regional scales (Messier *et al.*, 2010; Albert *et al.*, 2012; Violle *et al.*, 2012; Siefert *et al.*, 2015) and from organ-level traits to integrative traits involving several organs, as the latter tend to be more sensitive to the environment and show higher ITV as a result of local genetic adaptation and phenotypic plasticity (Marks, 2007; Siefert *et al.*, 2015). Thus, incorporating the variability of traits along environmental gradients among different organizational levels (family, species, population and individual) may help to elucidate how traits respond to environmental variation and thus improve trait-based models. For example, Reich *et al.* (2014) showed that accounting for ITV in gymnosperm needle longevity with latitude across boreal forests impacted significantly on carbon (C) cycling projections.

A related challenge is to understand how trait covariation changes at different ecological levels (organizational levels and spatial scales) (Levin, 1992; Chave, 2013). Previous work has shown that correlation patterns are not always conserved across scales. For example, several studies have failed to find some of the central LES tradeoffs, defined across species means at the global scale, when working at smaller spatial or organizational scales (Wright & Sutton-Grier, 2012; Laforest-Lapointe *et al.*, 2014; Niinemets, 2015; Messier *et al.*, 2016; Anderegg *et al.*, 2018). This is because traits that appear closely coordinated at certain scales may have different sensitivities to scale-dependent drivers of variation, which can effectively decouple them at finer scales (Messier *et al.*, 2016). These results have important implications for trait-based ecology: if we want to predict species responses to changing environmental conditions, we need to elucidate intraspecific trait covariance structures to understand the adaptive value of trait combinations in different environments. At the same time, we should be cautious when interpreting trait relationships across species as fundamental tradeoffs among functions and strategy dimensions. The study of trait correlation networks is a step forward in formalizing multiple factors shaping an integrated plant phenotype (Poorter *et al.*, 2014; Messier *et al.*, 2017) and allowing comparisons across scales.

The complexity of trait variation has usually been condensed in a few easily measured ('soft') traits that are not necessarily good predictors of demographic rates (Poorter *et al.*, 2008; Paine *et al.*, 2015; Yang *et al.*, 2018). For example, leaf mass per area (LMA), one of the most commonly measured traits, is usually weakly associated with growth rate, especially in adult plants (Wright *et al.*, 2010; Gibert *et al.*, 2016). Moving from 'soft' traits to more mechanistic ('hard') traits that have a clearer physiological basis and are likely to be stronger determinants of fitness should improve our capacity to elucidate vegetation dynamics under changing environmental conditions. This is particularly the case for drought-related impacts on forest function and dynamics (Skelton *et al.*, 2015; Sperry & Love, 2015; Brodribb, 2017), which are expected to increase in most regions of the Earth under climate change (Allen *et al.*, 2015).

Several studies have related hydraulic traits to plant performance under drought in terms of growth and mortality rates (Rowland *et al.*, 2015; Anderegg *et al.*, 2016; Choat *et al.*, 2018). Hydraulic traits define the efficiency of the plant water transport system, usually defined in terms of stem-specific hydraulic conductivity ( $K_S$ ) and its safety against failure under drought stress, typically characterized as the water potential at which 50% stem conductivity is lost as a result of xylem embolism ( $P_{50}$ ). In addition, allocation to sapwood cross-sectional area relative to leaf area (the Huber value, Hv) regulates supply capacity per unit of water demand, and it is thus a key component of plant hydraulic architecture (Mencuccini & Bonosi, 2001). It has been shown that plants can respond to drier conditions by increasing the resistance to xylem embolism (e.g. Blackman *et al.*, 2014), decreasing the leaf water potential at turgor loss in leaves (Bartlett *et al.*, 2012) and/or increasing their sapwood-to-leaf area ratio (Martínez-Vilalta *et al.*, 2009). Thus, these hydraulic traits can be used to describe the range of plant hydraulic strategies in diverse

communities (Skelton *et al.*, 2015) and may provide stronger insights into the drivers of forest dynamics than the more commonly measured 'soft' traits (Brodribb, 2017).

If trait variation across scales in commonly measured 'soft' traits remains poorly understood, knowledge is even more limited regarding hydraulic traits. A recent meta-analysis found that 33% of the variation in  $P_{50}$  was contributed by differences within species (Anderegg, 2015). However, part of this variability could be a result of methodological aspects (Cochard *et al.*, 2013) and several individual studies have shown low plasticity in embolism resistance across climatically contrasted populations (Maherali & DeLucia, 2000; Martínez-Vilalta *et al.*, 2009; Lamy *et al.*, 2011, 2014; López *et al.*, 2016). The degree of coordination between leaf economics traits and hydraulic traits is also a leading research subject. A universal 'fast-slow' whole-plant economics spectrum that integrates resource use strategies (for water, C and nutrients) across organs has been proposed (Reich, 2014), but the evidence remains mixed (Brodribb *et al.*, 2007; Blonder *et al.*, 2011; Markesteijn *et al.*, 2011; Méndez-Alonzo *et al.*, 2012; Sack *et al.*, 2013; Li *et al.*, 2015).

To address these critical issues, we studied the variability of a set of hydraulic, leaf and stem traits along a water availability gradient in six dominant tree species in Catalonia (northeastern Spain), focusing on the following questions:

(1) How much trait variation is observed and how is it distributed among levels of organization? We hypothesize that differences between families (Pinaceae vs Fagaceae) will explain the largest part of trait variability in this temperate system, although ITV will be substantial, especially for more integrative traits such as  $K_L$  and Hv.

(2) How do traits vary along the water availability gradient within and between species? We hypothesize that hydraulic traits will be more closely linked to water availability than are other stem and leaf traits. Most of the trait changes along the water availability gradient will entail species substitutions and, thus, the strength of trait-environment relationships will be weaker within than across species, reflecting lower capacity for functional adjustment within species.

(3) How are traits coordinated across and within species? Across species, we hypothesize the existence of a general 'fast-slow' strategy at the whole-plant level that combines LES and hydraulic traits (e.g. low LMA will be associated with high  $K_S$  and high vulnerability to embolism). At the same time, we expect that intraspecific correlation networks may differ from those across species because relatively weak evolutionary or physiological tradeoffs can be reversed as a result of plasticity within species.

## Materials and Methods

### Study site and sampling design

The study area included all the forested territory of Catalonia (northeastern Spain), encompassing 1.2 million ha, c. 38% of its total land area. Catalonia is very diverse both topographically and climatically: mean annual temperature ranges from 18°C (at the

southern coast) to 3°C (in the Pyrenees) and annual rainfall varies from 400 to >1500 mm (CDAC, <http://www.opengis.uab.cat/acdc/>). We selected six of the most dominant tree species in Catalonia (three Pinaceae and three Fagaceae), accounting for c. 75% of the total forest area (Gracia *et al.*, 2004; see also Supporting information Table S1): *Pinus sylvestris* L., *Pinus nigra* J.F.Arnold., *Pinus halepensis* Mill., *Fagus sylvatica* L., *Quercus pubescens* Willd. and *Quercus ilex* L. For each species, 15 plots from the Spanish forest inventory (IFN) were resampled in which the target species was dominant (minimum 50% of the total basal area), maximizing the water availability gradient occupied by each species in the study region. Water availability was quantified as the precipitation to potential evapotranspiration ratio (P : PET), for the spring–summer period (see later). Five plots per species were sampled for each of three species-specific P : PET ranges following a stratified random design (dry, corresponding to P : PET < 33<sup>rd</sup>/66<sup>th</sup> percentile and mild for the rest) (Figs S1, S2). Plots with the two highest stoniness values and those that had been managed during the last 14 years according to previous IFN surveys were discarded.

Within each plot, five nonsuppressed canopy trees of the target species with diameter at breast height (DBH) > 12.5 cm were randomly selected, all within 25 m of the centre of the plot. All samples and data were collected from May to December 2015. To minimize phenological variation in traits within species, species were sampled sequentially (*P. halepensis*, mid-May to end June; *Q. pubescens*, end June and July; *F. sylvatica*, August; *P. sylvestris*, September to mid-October; *Q. ilex*, mid-October to mid-November; *P. nigra*, mid-November to mid-December). From each tree, two branches (one for leaf measurements and the other for hydraulic measurements) were sampled from the exposed part of the canopy in the top half of the crown. Sampled branches were at least 70 cm long for *Pinus* spp., 150 cm for *Quercus* spp. and 80 cm for *Fagus*, to account for differences in the maximum length of xylem conduits (see later). Branches were transported to the laboratory inside plastic bags under cool and dark conditions and measurements were taken within 24 h.

## Environmental variables

At each plot, four soil samples (20 cm deep) were taken using a soil core at the four cardinal points at 5 m distance from the centre of the plot. The topsoil (O horizon) was removed to exclude the organic deposit and litterfall, and the four samples were merged. The following variables were measured on each pooled sample: N-NO<sub>3</sub> concentration (colorimetric method; Keeney & Nelson, 1982), phosphorus (P) content (available P-Olsen P; Olsen & Sommers, 1982), soil humidity (gravimetric soil water content; Gardner, 1986), organic matter fraction (organic C content estimated with acid dichromate oxidation method; Nelson & Sommers, 1982) and soil texture classes defined by the USDA system (sedimentation-Robinson pipette; Gee & Or, 2002). To integrate the different components of soil texture into one single variable, the exponent of the Saxton equation (Saxton *et al.*, 1986) was calculated as follows:

$$b = -3.140 - 0.00222 (\% \text{ clay})^2 - 3.484 \times 10^{-5} (\% \text{ sand})^2 (\% \text{ clay}) \quad \text{Eqn 1}$$

where less negative values of *b* indicate sandy soils with lower soil water retention capacity.

Forest structure data for each plot were also available from the last Spanish forest inventory (IFN4) that was conducted over the same time period as our sampling. Forest structural data included total plot basal area, stand density, mean DBH and the 90<sup>th</sup> percentile for height of all trees in the plot. Climate data were obtained from the Climatic Digital Atlas of Catalonia (Ninyerola *et al.*, 2005), a collection of digital maps at 200 × 200 m resolution including average annual radiation, mean annual temperature, minimum annual temperature and annual precipitation for the period 1951–2010. PET values were calculated according to the Hargreaves–Samani method (Hargreaves & Samani, 1982) and used to estimate P : PET for the spring–summer period and P : PET for the summer period.

## Leaf traits and wood density

Standard protocols (Pérez-Harguindeguy *et al.*, 2013) were followed for all trait measurements (Table 1). Previous-year needles (conifers) and current-year leaves (broadleaves) were selected to measure fully expanded leaves. Before measurements, twigs with leaves were cut under water and placed into flasks with the cut end submerged in deionized water in the dark overnight.

Leaf mass per area is a measure of biomass investment in leaves per unit light interception and gas exchange (Poorter *et al.*, 2009). For LMA determinations, 20 leaves were randomly selected, scanned and their areas were measured with IMAGEJ software (Wayne Rasband-National Institute of Health, Bethesda, MD, USA). Afterwards, samples were oven-dried at 60°C and weighed, and LMA was calculated as leaf dry mass/fresh area.

The Hv is the ratio of cross-sectional sapwood area to subtended leaf area, and it can therefore be viewed as the ratio of hydraulic and mechanical investment costs over the expected gains obtained by leaf display. Leaves from terminal branches (65 cm long from the tip) were oven-dried and weighed, and LMA was used to convert the total dry weight of the distal leaves of each branch into total branch leaf area. In order to calculate branch level Hv, and to make values comparable across species, maximum leaf area was estimated, taking into account species phenology and the time of sampling. Sapwood area was obtained through measuring total xylem area on digital images of stained (safranin-astra blue) 15–20 µm thin sections in IMAGEJ (Wayne Rasband-National Institute of Health).

We used leaf C isotope composition (δ<sup>13</sup>C) and leaf nitrogen (N) concentrations to further characterize leaf functioning. Less negative δ<sup>13</sup>C values suggesting lower discrimination against the heavier <sup>13</sup>C are indicative of greater stomatal control and water-use efficiency (Farquhar *et al.*, 1989), whereas higher leaf N concentrations are usually associated with higher photosynthetic capacity because of the high N content of photosynthetic machinery (Evans, 1989). Leaf δ<sup>13</sup>C and N were determined



using a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd, Crewe, UK) at the UC-Davis Stable Isotopes Facility (Davis, CA, USA). Samples were previously oven-dried at 60° C for 4 d, grounded with a Retsch MM400 ball mill (Verder Group, Haan, Germany) and placed in tin capsules for analysis. C stable isotope concentrations were expressed in relation to the Pee-Dee Belemnite standard.

Leaf osmotic potential ( $\Psi_0$ ) was measured with a VAPRO 5500 vapor pressure osmometer (Wescor, Logan, UT, USA). Leaves were wrapped in foil to limit condensation and evaporation, submerged in liquid nitrogen for 2 min and sealed in a plastic zip bag under ambient conditions. After letting them defrost, they were put inside a syringe and squeezed until 10  $\mu$ l of sap were obtained. Finally,  $\Psi_0$  was used to predict the leaf water potential at which leaf cells lose turgor, closing their stomata and ceasing gas exchange and growth ( $P_{\text{dp}}$ ) (Brodribb *et al.*, 2003), according to the equation described in Bartlett *et al.* (2012):

$$P_{\text{dp}} = 0.832\Psi_0 - 0.631 \quad \text{Eqn 2}$$

Wood density (WD) is considered a central trait shaping the wood economics spectrum (Chave *et al.*, 2009). We measured WD on one stem core per individual extracted using a hand increment borer (5 mm diameter; Suunto, Vantaa, Finland). The core was sealed in plastic tubes upon collection and taken to the laboratory under cold conditions. Fresh core volume of all wood was calculated after removing the bark by the dimensional method, measuring its total length and its diameter using a caliper. Cores were then oven-dried at 100°C for 48 h and weighed. WD was calculated as the oven-dry mass divided by fresh volume.

## Hydraulic traits

Before hydraulic measurements, maximum vessel length was estimated using the air infiltration technique (Ewers & Fisher, 1989) on eight 2 m branches per species. We pumped compressed air (c. 0.15 MPa) through the branches with their basal end immersed in water and successively shortened the stem until bubbling was observed. Because compressed air at low pressures cannot pass through vessel end walls, the bubbling indicated the presence of open xylem conduits. The resulting estimates of maximum conduit length were used to decide the minimum length of the sampled branches (see the Study site and sampling design section earlier).

Vulnerability curves were established by measuring the hydraulic conductivity of stem segments at different water potentials, using a variation of the bench dehydration method (Sperry & Tyree, 1988; Cochard *et al.*, 2013; Choat *et al.*, 2015). Hydraulic conductivity was measured using a commercial XYL'EM apparatus (Bronkhorst, Montigny-les-Cormeilles, France) as the ratio between the flow through the stem segment and the pressure gradient (5 kPa). The initial hydraulic conductivity ( $K_i$ ) was measured in three subsamples (segments) per branch that were excised underwater at the terminal part of the

shoots (Martin-StPaul *et al.*, 2014). An initial cut was applied to allow xylem tension in the branch segment to relax before measurement, avoiding artefacts associated with the cutting under tension (Wheeler *et al.*, 2013). After the segments were cut again to their final size (c. 2 cm in length), their proximal ends were connected to the tubing system of the XYL'EM, which was filled with deionized filtered water with 10 mM KCl and 1 mM  $\text{CaCl}_2$  that had been previously degassed using a membrane contactor (Liqui-Cell Mini-Module membrane 1.7  $\times$  5.5; Charlotte, NC, USA). After measuring the initial conductivity, the segments were flushed once at 0.15 MPa for 10 min (for *Quercus* spp. and *F. sylvatica*) or held in the solution under partial vacuum for 48 h (for *Pinus* spp., as flushing conifer segments often results in the pit membranes being permanently pushed against tracheid cells walls) in order to measure their maximal conductivity ( $K_{\text{max}}$ ) as described earlier. The values of  $K_i$  and  $K_{\text{max}}$  were used to compute the percentage loss of hydraulic conductivity (PLC). The previous measurements were repeated a second time on a different set of stem segments after branches had been dehydrated on the bench to obtain PLC estimates at lower water potentials. The timing of this second measurement was adjusted for different species and branches (between 2 and 8 d) to cover a wide range of PLC values. The tubing system was regularly cleaned using 10% bleach solution for at least 20 min to prevent microorganism growth and, afterwards, flushed with a degassed solution. Additionally, we used the apical part of each measured twig segment to measure water potential ( $\Psi$ ) with a Scholander pressure chamber (Solfranc Tecnologias, Tarragona, Spain).

To fit vulnerability curves to each set of PLC and water potential measurements, the following sigmoid function was used (Pammenter & Willigen, 1998):

$$\text{PLC} = 100 / (1 + \exp(a(\Psi - P_{50}))) \quad \text{Eqn 3}$$

where  $\Psi$  is the water potential,  $a$  is the slope of the curve (and thus determines the rate at which conductivity is lost as water potential declines), and  $P_{50}$  determines the position of the curve on the abscissa and gives the pressure causing 50% loss of conductivity. Parameters were estimated by fitting a separate nonlinear mixed model for each species, using the NLME R package (Pinheiro *et al.*, 2018). The model accounted for individual nested in plot as a random effect on coefficient  $P_{50}$ . Preliminary analyses confirmed that this model structure provided the best fit to the data.

In addition, all distal leaves of each segment were removed to determinate their area as explained above. Leaf-specific hydraulic conductivity ( $K_L$ ) was calculated as  $K_{\text{max}}$  divided by the distal leaf area supported. Similarly, stem-specific hydraulic conductivity ( $K_S$ ) was calculated as  $K_{\text{max}}$  divided by cross-sectional sapwood area.

## Statistical analyses

To assess trait variability, the quartile coefficient of dispersion (QCD) was calculated for each trait as the ratio between half the interquartile range ((Q3 – Q1)/2) and the average of the quartiles

$((Q1 + Q3)/2)$ . QCD was used as a more robust measure of dispersion than the coefficient of variation (CV), as the latter is not appropriate for datasets including isotopic measurements (Brendel, 2014) or log-transformed data (Canchola *et al.*, 2017) (see also the Table S2). To understand the distribution of variability for each trait, we used different sets of linear mixed models, always fitting separate models for each trait. In the first ones, family, species and population were introduced as nested random factors to assess how trait variability was distributed among these different levels of organization. In the second ones, models were fitted separately for each family, and included only species and population (nested) to assess trait variability among and within species (within each family). All variables were checked for normality and log<sub>e</sub>-transformed whenever required to ensure normality.

Before exploring the effect of environmental factors on trait variation, three separate principal component analyses (PCAs) were performed to summarize soil, forest structure and climate data (Fig. S3). As before, all variables were checked for normality and log<sub>e</sub>-transformed if required. For further analyses, the two most orthogonal variables showing the highest axes loading in each PCA were selected as integrated measures of environmental predictors. Coefficient *b* from the Saxton equation (Eqn 1) and soil P were selected to describe soil characteristics, mean tree DBH and total plot basal area to describe forest structure, and spring–summer P : PET and annual radiation to describe the climate. A first mixed model for each trait was fitted starting with the ‘saturated’ model, including all six environmental variables as fixed explanatory variables (without interactions). We included plot nested in species as random effects on the intercept of the model. Preliminary analyses showed that including a random species effect on the slopes did not improve model fit. This model was simplified stepwise, removing the least significant term until a minimal adequate model with the lowest Akaike information criterion (AIC) was obtained. Models within two AIC units were considered equivalent in terms of fit and the simplest one was selected (Zuur *et al.*, 2009).

To explore specifically the variability of each trait along the P : PET gradient imposed by our sampling design, a second mixed model was fitted for each trait. To separate the intraspecific from the interspecific component of trait responses to P : PET, we split P : PET into two additive variables which were included as separate fixed factors in the model: mean P : PET at the species level and centred P : PET. The latter variable was calculated as the difference between plot P : PET and the average P : PET for the corresponding species. We also included plot nested within species as a random effect on the intercept. As before, preliminary analyses showed that including a random species effect on the slope did not improve model fit. Model selection was carried out as described earlier. In all cases, the residuals of the selected models showed no obvious pattern and were approximately normally distributed. Linear mixed effects models were fitted using the LME4 package (Bates *et al.*, 2015).

Finally, to characterize trait coordination within and between species, statistically significant correlations among traits were graphically represented using trait covariation networks with the IGRAPH package (Csardi & Nepusz, 2006). Traits were

represented as nodes and their correlation as the edges linking them. Two indicators of network centrality were calculated for each trait: the degree (*D*), defined as the number of edges of a node and the weighted degree (*D<sub>w</sub>*), defined as the sum of all significant coefficients of correlation of a node (Table S5). In these latter analyses, all traits were log<sub>e</sub>-transformed to improve the linearity of relationships. All analyses were carried out using R statistical software v.3.3.2 (R Core Team, 2017).

## Results

### Magnitude and distribution of trait variability

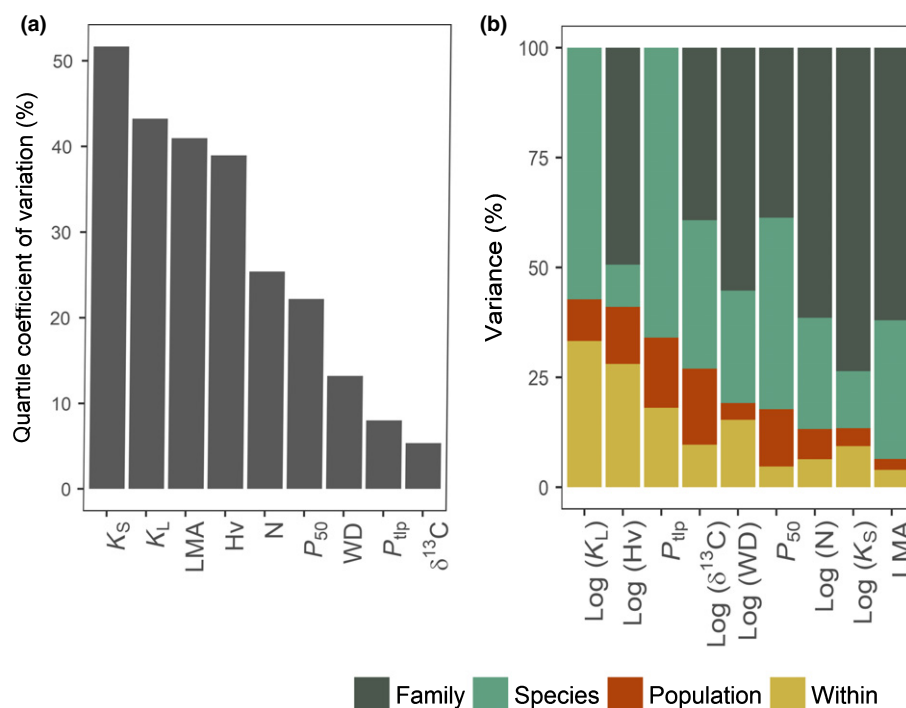
Most trait variation occurred between families (Pinaceae vs Fagaceae), with the exception of *K<sub>L</sub>* and *P<sub>tlp</sub>* for which the contribution of family was close to zero (Fig. 1b). Pinaceae tended to have higher LMA, Hv and  $\delta^{13}\text{C}$  than Fagaceae, whereas the opposite was true for leaf N, WD, *K<sub>S</sub>* and *P<sub>50</sub>* (Fig. S4). Overall, the proportion of variance explained at the intraspecific level (among and within populations) was, on average, 23.11% (Fig. 1b). Within Pinaceae, *K<sub>S</sub>*, *K<sub>L</sub>*, Hv, WD and  $\delta^{13}\text{C}$  showed a higher variability within than among species, whereas in Fagaceae this was only the case for Hv (Fig. S5). Other traits, such as *P<sub>50</sub>*, showed substantial variability within families (4.51 MPa range within Pinaceae and 3.84 MPa range within Fagaceae) but most of this variance occurred across species (Table S2; Fig. S5). *K<sub>S</sub>*, *K<sub>L</sub>*, LMA and Hv were the most variable traits, whereas  $\delta^{13}\text{C}$ , *P<sub>tlp</sub>* and WD showed the least variation (Fig. 1a).

### Trait responses along a water availability gradient

Traits responded differently to environmental factors (Table 2). Regarding soil properties, only soil P concentration showed a significant effect (positive) on LMA. As for stand structure, mean DBH had a strongest predictive effect across all models. Plots with larger trees on average were associated with lower LMA, lower WD, lower Hv and lower *K<sub>L</sub>*. Stand basal area did not have significant effects on any trait. Finally, regarding climatic variables, high annual radiation was associated with leaves with high LMA and high (less negative)  $\delta^{13}\text{C}$ . Plots with higher P : PET values had trees with more negative  $\delta^{13}\text{C}$ , lower Hv and less negative *P<sub>tlp</sub>*. Overall, environmental variables at the plot level were not strong predictors of trait variation, as shown by relatively low values of the marginal *R*<sup>2</sup> (variation explained by the fixed effects) (Table 2). The fact that conditional *R*<sup>2</sup> values (Table 2) were normally much higher indicates that a large proportion of the variance in all traits is explained by differences among species and plots not captured by the environmental variables included in our analysis. Similar results were obtained if we used PCA axes as fixed factors describing environmental variation in models instead of individual variables (Table S3).

When we specifically explored the variability of each trait along the water availability (P : PET) gradient, considering both species means and plot-scale deviations from the means (centred values), higher marginal *R*<sup>2</sup> values and generally stronger effects were obtained (cf. Table S4). Significant relationships between

**Fig. 1** (a) Quartile coefficient of dispersion of the studied traits across all measurements of the study; (b) variance partitioning across different ecological levels of organization. 'Within' denotes variance between individuals of the same population. Traits are ordered (left to right) from higher to lower total variation in (a), and from higher to lower percentage variation within species in (b). LMA, leaf mass per area; N, leaf nitrogen concentration;  $\delta^{13}\text{C}$ , leaf carbon isotope composition; WD, wood density; Hv, Huber value, sapwood to leaf area ratio;  $K_L$ , leaf-specific xylem hydraulic conductivity;  $K_S$ , stem-specific xylem hydraulic conductivity;  $P_{50}$ , pressure causing 50% xylem embolism;  $P_{tlp}$ , leaf water potential at turgor loss point.



**Table 1** Traits measured in this study.

Trait	Symbol	Units
Leaf mass per area	LMA	$\text{kg m}^{-2}$
Leaf nitrogen concentration	N	$\text{mg g}^{-1}$
Leaf carbon isotope composition	$\delta^{13}\text{C}$	‰
Wood density (stem)	WD	$\text{g cm}^3$
Huber value, sapwood to leaf area ratio (branch)	Hv	$\text{cm}^2 \text{m}^{-2}$
Leaf-specific xylem hydraulic conductivity (branch)	$K_L$	$\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$
Stem-specific xylem hydraulic conductivity (branch)	$K_S$	$\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$
Pressure causing 50% xylem embolism (branch)	$P_{50}$	MPa
Leaf water potential at turgor loss point	$P_{tlp}$	MPa

[Correction added after online publication 8 February 2019: the units for Leaf mass per area in Table 1 have been corrected.]

P : PET and traits across species were consistent with the results reported in the previous paragraph, but we also found a positive relationship between P : PET and  $P_{50}$  (which was only marginally significant in the previous analysis) and a positive relationship with leaf N concentrations (Fig. 2). Importantly, trait–environment relationships were scale-dependent and when these patterns were analysed within species, we only found significant relationships between centred P : PET and Hv and  $P_{tlp}$ . In these two cases, the relationships had the same (negative) sign but shallower slopes than the corresponding relationships across species (Fig. 2; Table S4). Similar results were obtained when the mean DBH, the strongest explanatory variable in the initial mixed model (cf. previous paragraph), was included as a fixed factor in this latter model (not shown).

### Trait correlation networks

Trait coordination differed within- and among- species (Fig. 3). When species means were considered, LMA and Hv were the traits showing highest values of centrality across species (Table S5). These two traits were positively related to each other and tightly linked to leaf N,  $\delta^{13}\text{C}$  and  $P_{50}$ , so that higher allocation to sapwood area relative to leaf area was correlated with a greater construction cost per unit leaf area, lower N, higher water-use efficiency (less negative  $\delta^{13}\text{C}$  values) and higher cavitation resistance (more negative  $P_{50}$ ).  $P_{tlp}$  and  $K_L$  also showed a positive relationship. Surprisingly,  $K_L$  and  $K_S$  were unrelated across species, although a consistent, positive relationship appeared when species were analysed separately (Fig. 3).

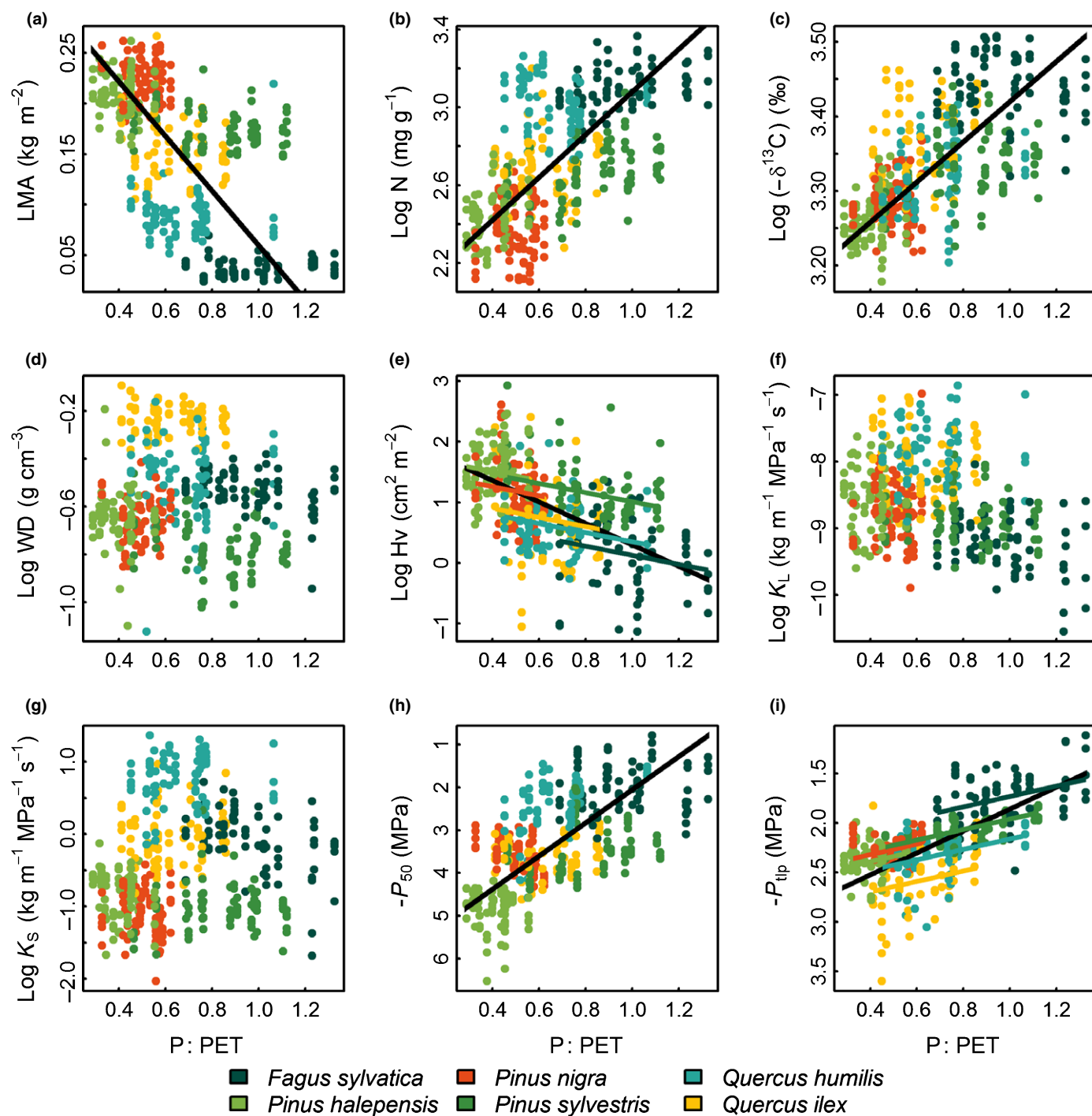
When analysing trait coordination within species, the strong LMA–Hv relationship observed across species was only significant in one species (*Q. ilex*). At the intraspecific level, the negative correlation between LMA and  $-\delta^{13}\text{C}$  and the positive correlation between  $K_S$  and  $K_L$  were the only relationships present in all cases (Fig. 3).  $K_L$  showed the highest centrality in two out of the three measured gymnosperms, whereas it was never central in angiosperms. On the other hand, LMA was the trait with the highest centrality in two out of three studied angiosperm species. However, caution is needed when considering these results, owing to the limited number of species sampled within each family. When centrality was expressed as a simple count of the number of significant correlations ( $D$ ),  $\delta^{13}\text{C}$  and  $P_{tlp}$  also appeared particularly important, especially in Fagaceae (Table S5). Finally, taking into account the overall network, *P. sylvestris*, *F. sylvatica* and *Q. ilex* were the species showing more correlations among traits and the highest  $D_w$  (Table S5).

**Table 2** Results of the linear mixed models examining the relationships between traits and environmental variables characterizing the soil, the climate and the stand structure.

	LMA	Log N	Log(− $\delta^{13}\text{C}$ )	Log WD	Hv	$K_L$	$K_S$	− $P_{50}$	− $P_{\text{tip}}$
Fixed parts									
Soil P	<b>0.08</b> (0.02 – 0.13)*	−0.08 (−0.17 – 0.01)	ni	0.08 (−0.00 – 0.17)	ni	ni	ni	ni	ni
Log ( <i>b</i> Saxton)	ni	ni	ni	0.05 (−0.01 – 0.12)	ni	ni	ni	ni	−0.03 (−0.13 – 0.07)
Log (DBH <sub>mean</sub> )	−0.07 (−0.12 to −0.01)*	0.09 (−0.00 – 0.17)	0.12 (0.00 – 0.24)	−0.11 (−0.19 to −0.03)**	−0.14 (−0.26 to −0.01)*	−0.14 (−0.24 to −0.03)*	−0.08 (−0.16 to −0.00)	ni	ni
Basal area	−0.05 (−0.10 – 0.01)	ni	ni	0.01 (−0.06 – 0.09)	ni	ni	ni	0.08 (−0.03 – 0.20)	ni
Annual radiation	<b>0.06</b> (0.01 – 0.10)*	ni	−0.23 (−0.33 to −0.13)***	ni	0.09 (−0.01 – 0.20)	0.07 (−0.02 – 0.17)	ni	ni	ni
Log (P : PET)	ni	ni	0.25 (0.09 – 0.41)**	ni	−0.27 (−0.44 to −0.10)**	ni	ni	−0.18 (−0.35 to −0.02)	−0.36 (−0.53 to −0.20)***
Random part									
$\sigma^2$	0	0.009	0.001	0.009	0.178	0.153	0.087	0.071	0.024
$\tau_{00}$ , PLOT:SP	0	0.009	0.001	0.002	0.065	0.039	0.036	0.193	0.017
$\tau_{00}$ , SP	0.005	0.084	0.002	0.035	0.134	0.216	0.521	0.775	0.053
$R^2$ marginal	0.02	0.01	0.22	0.01	0.14	0.03	0	0.02	0.14
$R^2$ conditional	0.94	0.91	0.84	0.8	0.59	0.64	0.86	0.93	0.78
Observations	444	444	444	444	439	444	444	444	425

A different mixed effects model including all environmental variables in the fixed part and plot nested within species in the random part was fitted for each trait. The model's standardized coefficients including confidence intervals (in brackets) are shown. Significant correlations (\*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ ) are shown in bold. Information on the random effect variances ( $\sigma^2$ , total;  $\tau_{00}$ , PLOT:SP, within-species;  $\tau_{00}$ , SP, cross-species), the proportions of explained variance by fixed effects ( $R^2$  marginal) and explained variance by fixed and random effects ( $R^2$  conditional) is also provided. DBH<sub>mean</sub>, plot mean diameter at the breast height; *b* Saxton, *b* Saxton coefficient; soil P, soil phosphorus content; P : PET, precipitation to potential evapotranspiration ratio; ni, not included in the best model; LMA, leaf mass per area; N, leaf nitrogen concentration;  $\delta^{13}\text{C}$ , leaf carbon isotope composition; WD, wood density; Hv, Huber value, sapwood to leaf area ratio;  $K_L$ , leaf-specific xylem hydraulic conductivity;  $K_S$ , stem-specific xylem hydraulic conductivity;  $P_{50}$ , pressure causing 50% xylem embolism;  $P_{\text{tip}}$ , leaf water potential at turgor loss point.





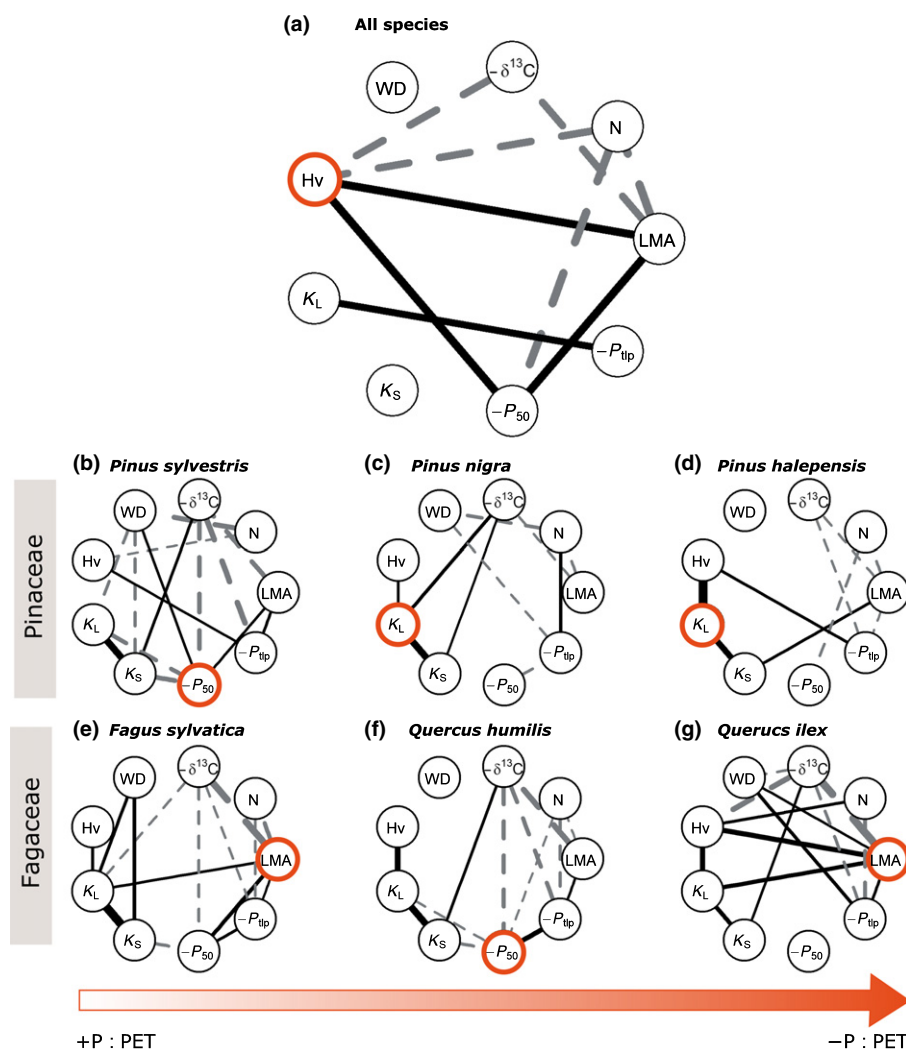
**Fig. 2** Relationship between water availability (in terms of the precipitation to potential evapotranspiration ratio, P : PET) and (a) leaf mass per area, (b) leaf nitrogen concentration, (c) leaf carbon isotope composition, (d) wood density, (e) Huber value, sapwood to leaf area ratio, (f) leaf-specific xylem hydraulic conductivity, (g) stem-specific xylem hydraulic conductivity, (h) pressure causing 50% xylem embolism and (i) leaf water potential at turgor loss point. The black regression lines give the overall cross-species relationships, and the coloured lines give the corresponding within-species relationships, when significant ( $P < 0.05$ ). Variables were  $\log_e$ -transformed whenever required to satisfy normality assumptions. LMA, leaf mass per area; N, leaf nitrogen concentration;  $\delta^{13}\text{C}$ , leaf carbon isotope composition; WD, wood density; Hv, Huber value, sapwood to leaf area ratio;  $K_L$ , leaf-specific xylem hydraulic conductivity;  $K_S$ , stem-specific xylem hydraulic conductivity;  $P_{50}$ , pressure causing 50% xylem embolism;  $P_{tlp}$ , leaf water potential at turgor loss point. [Correction added after online publication 8 February 2019: the units for LMA on the y-axis of panel (a) have been corrected.]

## Discussion

We found that traits varied primarily between tree families but that ITV also accounted for a relevant amount of total variation,

especially in more integrative traits ( $K_L$ , Hv). Most study traits responded to water availability, with increasing N,  $P_{50}$  and  $P_{tlp}$  and decreasing LMA,  $\delta^{13}C$  and Hv with P : PET across species. However, at the intraspecific level, we only found trait variation





**Fig. 3** (a–g) Trait correlation networks across species ( $n = 6$ ) (a) and for each studied species separately (b–g). Solid black and grey dashed edges show positive and negative correlations, respectively. Correlation strength is represented by edge thickness. Only significant correlations are shown ( $P < 0.05$ ). Traits identified by red circles show the highest centrality value in terms of weighted degree (the sum of all the significant coefficients of correlation of a node). All traits were  $\log_e$ -transformed before analysis. LMA, leaf mass per area; N, leaf nitrogen concentration;  $\delta^{13}\text{C}$ , leaf carbon isotope composition; WD, wood density; Hv, Huber value, sapwood to leaf area ratio;  $K_L$ , leaf-specific xylem hydraulic conductivity;  $K_S$ , stem-specific xylem hydraulic conductivity;  $P_{50}$ , pressure causing 50% xylem embolism;  $P_{tlp}$ , leaf water potential at turgor loss point.

along the water availability gradient for Hv and  $P_{tlp}$ . Finally, trait coordination was scale-dependent and we did not find clear evidence of a single, dominant axis of variation reflecting a fast-slow, whole-plant economics spectrum.

### Magnitude and distribution of trait variability

Our results show that traits differ substantially in their variability along the same environmental gradient, with an order of magnitude difference in the quartile coefficient of dispersion between the most variable ( $K_S$  and  $K_L$ ) and the least variable traits ( $\delta^{13}\text{C}$  and  $P_{tlp}$ ). The high variability of  $K_S$  and  $K_L$  agrees with previous studies across species (Maherali *et al.*, 2004; Martínez-Vilalta *et al.*, 2004; Gleason *et al.*, 2015) and may be caused by their high sensitivity to small differences in wood anatomy (particularly conduit diameter), which varies substantially across and within species (Tyree *et al.*, 1994; Sperry *et al.*, 2008). The higher variability of  $K_S$  relative to  $K_L$  probably reflects that the latter is normalized by water demand in terms of leaf area. More generally, however, the ecological implications of this high variability in xylem transport capacity, both

within and among species, remains to be elucidated, particularly considering that in our study  $K_S$  and  $K_L$  did not respond consistently to water availability. On the other hand,  $P_{tlp}$  showed very low variability in comparison to other hydraulics traits, also in agreement with previous findings (Mencuccini *et al.*, 2015; Bartlett *et al.*, 2016).

Not surprisingly, trait variability was mostly distributed across families, reflecting the contrasting trait syndromes between angiosperm and gymnosperm clades (Wright *et al.*, 2004; Chave *et al.*, 2009; Carnicer *et al.*, 2013). Our results also confirm previous findings for hydraulic traits, with higher Hv, lower  $K_S$  and higher resistance to embolism in conifers relative to angiosperm trees (Becker *et al.*, 1999; Choat *et al.*, 2012; Gleason *et al.*, 2015). The high proportion of variation attributed to the family level for  $K_S$  is explained by xylem conduit properties, as unicellular conifer tracheids are substantially narrower and more than an order of magnitude shorter than angiosperm vessels (Sperry *et al.*, 2006). Besides the direct effect of these different dimensions on  $K_S$ , the fact that we measured relatively short segments implies that our  $K_S$  estimates corresponded mostly to lumen conductivity for the Fagaceae and to total conductivity (lumen and end wall)

for Pinaceae species. Interestingly, the family effect disappeared when xylem conductivity was normalized by leaf area ( $K_L$ ) because conifers also tend to have more sapwood per unit leaf area (higher Hv; Fig. S4) (see also Becker *et al.*, 1999).

Intraspecific trait variability contributed to a substantial amount of the total variance (from 6% to 42% depending on the trait). This is consistent with a growing body of evidence showing that ITV is relevant (Albert *et al.*, 2012; Laforest-Lapointe *et al.*, 2014), especially when we move from organ-specific traits (leaves, stems or roots) to more integrative traits involving several organs (e.g.  $K_L$ , Hv) (Siefert *et al.*, 2015). Studies addressing ITV in hydraulic traits are less frequent (but see Martínez-Vilalta *et al.*, 2009; Wortemann *et al.*, 2011; Lamy *et al.*, 2014; Hajek *et al.*, 2016). In line with our results, Hv and  $K_L$  have been reported to be among the most plastic hydraulic properties in pines (DeLucia *et al.*, 2000; Martínez-Vilalta *et al.*, 2009) whereas other traits such as  $P_{50}$  usually show low plasticity (Maherali & DeLucia, 2000; Martínez-Vilalta *et al.*, 2009; Lamy *et al.*, 2014; López *et al.*, 2016). Further studies are needed to investigate whether these patterns are generalizable across other plant families. It should also be noted that we probably underestimated the magnitude of ITV because we did not cover the whole species distribution range, species were sampled sequentially to minimize phenological variation within species, and we always selected healthy-looking mature trees with sun-exposed branches according to standard trait sampling protocols (Pérez-Harguindeguy *et al.*, 2013). These factors, however, would also affect total trait variation and it remains unclear what their impact would be on the percentage contribution of ITV.

### Trait responses along a water availability gradient

In agreement with findings reported in other studies (Vilà-Cabrera *et al.*, 2015; Anderegg *et al.*, 2018), trait–environment relationships were not very tight, suggesting that unaccounted species-specific differences and/or other plot variables not included in our study were stronger drivers of trait variability. Mean DBH was the strongest determinant of trait variation. Specifically, plots with larger trees on average tended to have lower LMA, WD, Hv and  $K_L$ , in line with previous findings (Laforest-Lapointe *et al.*, 2014; Gleason *et al.*, 2018). The effect of P : PET, our target environmental factor, was significant or marginally significant for  $\delta^{13}\text{C}$ , Hv,  $P_{\text{dp}}$  and  $P_{50}$ , but not for LMA, N or WD when controlling for the effect of other environmental factors. This indicates that hydraulic and water-related traits responded more strongly to water availability than did LES or other stem traits, as hypothesized.

When we assessed the overall response of each trait to P : PET, without accounting for the effect of other environmental variables that covaried along the environmental gradient studied, a higher proportion of trait variance was explained, because species means were explicitly included in the model (Table S4). In this broader assessment, LMA and N were also related to water availability, besides the hydraulic/water relations variables identified in the previous analysis. Wetter sites were associated with species with leaf traits related to acquisitive resource strategies (low LMA and high N). Several studies have shown that LMA tends to be

higher at drier sites as a result of water stress adaptation through increasing wilting resistance (Schulze *et al.*, 1998; Cunningham *et al.*, 1999). Regarding the relationship between N and water availability, contrasting results have been reported. Although some studies have reported that species from drier sites present higher N leaf concentration to enhance water conservation during photosynthesis (Wright & Westoby, 2002), others have found no general relationship (Killingbeck & Whitford, 1996; Vilà-Cabrera *et al.*, 2015).

Vulnerability to xylem embolism was lower (more negative  $P_{50}$ ) in species occupying drier sites, consistent with the notion that cavitation resistance is a key determinant of species distributions (Maherali *et al.*, 2004; Jacobsen *et al.*, 2007; Martínez-Vilalta *et al.*, 2012; Choat *et al.*, 2012; Blackman *et al.*, 2014; Trueba *et al.*, 2017; Li *et al.*, 2018; Skelton *et al.*, 2018). Similarly, another key drought tolerance trait,  $P_{\text{dp}}$ , also showed a significant relationship with P : PET across species, with lower (more negative)  $P_{\text{dp}}$  associated with drier habitats, allowing the maintenance of leaf turgor and gas exchange under drier conditions (Brodribb *et al.*, 2003; Lenz *et al.*, 2006; Bartlett *et al.*, 2012). This did not, however, prevent an increase in water-use efficiency (less negative  $\delta^{13}\text{C}$  values) and increased allocation to sapwood area relative to leaf area (Hv) at drier sites, consistent with previous reports (Warren *et al.*, 2001; Martínez-Vilalta *et al.*, 2004, 2009; Gebrekirstos *et al.*, 2011). Interestingly, species hydraulic efficiency ( $K_S$ ,  $K_L$ ) did not vary consistently along the water availability gradient. Overall, our results across species suggest that increasing tolerance to hydraulic dysfunction in drier sites implies increasing C costs per unit leaf area in terms of leaf and sapwood construction.

Importantly, trait–environment relationships were scale-dependent (Anderegg *et al.*, 2018) and, as hypothesized, relationships within species were generally weaker than across species. Hv and  $P_{\text{dp}}$ , two of the three traits with higher percentage ITV, were the only traits that responded to P : PET within species. These two intraspecific relationships had the same sign but shallower slopes than the corresponding relationships with P : PET among species, which probably reflects lower capacity for hydraulic adjustment within than among species as a result of relatively fixed drought response strategies at the species level. This result highlights the importance of Hv and  $P_{\text{dp}}$  in shaping plastic responses along water availability gradients. Lower leaf area per unit of sapwood (which reduced water demand) and osmotic adjustment may be needed to balance water and C costs under reduced water availability in the context of relatively constant hydraulic safety thresholds within species, measured here as stem  $P_{50}$ . This is consistent with the view that  $P_{50}$  is an (evolutionarily) canalized trait buffered against genetic and environmental variation (Lamy *et al.*, 2014). Overall, adjustments along the water availability gradient in the six species studied rely more on changes in stomata closure and resource allocation between sapwood and leaf area than changes in hydraulic safety and efficiency, consistent with previous results comparing pine populations (Mencuccini & Grace, 1995; Mencuccini & Bonosi, 2001; Poyatos *et al.*, 2007; Martínez-Vilalta *et al.*, 2009).

## Trait correlation networks

To our knowledge, our study is the first attempt to test simultaneously the covariation between traits related to leaf economics (LMA, N), xylem hydraulics in terms of safety and efficiency ( $P_{50}$ ,  $K_S$ ), allocation ( $K_L$ , HV) and traits related to leaf gas exchange ( $\delta^{13}\text{C}$ ,  $P_{\text{dp}}$ ), at both the interspecific and intraspecific levels. We found weak evidence for the existence of a unique coordination between hydraulics and more standard leaf and stem traits, which would be required for the existence of universal, resource use strategies at the whole-plant level (our last hypothesis, cf. Reich (2014)). In our study, species with conservative leaf economic strategies (i.e. higher LMA) presented a safer xylem (lower  $P_{50}$ ), possibly to support longer leaf life spans (Wright *et al.*, 2004). However, this interpretation should also consider that species occupying drier sites are also likely to be exposed to lower water potentials, which would affect their hydraulic safety margins and possibly result in higher hydraulic risk in drier locations. On the other hand, although higher LMA species also showed higher Hv, this pattern did not result in any relationship with xylem transport efficiency (either  $K_S$  or  $K_L$ ). This lack of a universal 'fast-slow' whole-plant economics spectrum is reinforced when we assess trait covariation at the intraspecific level. We provide evidence that rather than a single dominant axis of 'fast-slow' plant economics spectrum, multiple combinations of traits are possible depending on the species and the environment. Caution is thus needed when interpreting the comparatively simple trait covariation structures revealed in global studies using relatively few traits (Díaz *et al.*, 2016), and comprehensive assessments including wider sets of traits may improve our ability to represent the patterns underlying the huge diversity in plant form and function.

The increase in water-use efficiency (estimated from  $\delta^{13}\text{C}$ ) with increasing LMA was the only correlation present in all studied trait networks. This relationship is commonly reported (Körner *et al.*, 1991; Hultine & Marshall, 2000) and it is probably a result of an increase in length in the internal diffusion pathway from the stomata to the chloroplasts reducing carbon dioxide supply at the site of carboxylation (Evans *et al.*, 1986). We did not find support for a tradeoff between hydraulic safety and efficiency across species and only in two cases within species, consistent with a recent global synthesis that found that many species presented low safety and low efficiency (Gleason *et al.*, 2015). At the intraspecific level, of the two traits that responded to water availability at the intraspecific level, Hv was typically loosely linked to the rest of the trait network (except in *Q. ilex*), whereas  $P_{\text{dp}}$  retained a more central role. Higher leaf tolerance to low water potentials (more negative  $P_{\text{dp}}$ ) was associated with higher water-use efficiency (less negative  $\delta^{13}\text{C}$ ) and higher leaf construction costs (higher LMA) in most species, suggesting an adaptation to drier and hotter conditions (Wright *et al.*, 2005). It should be noted, however, that our results on trait coordination across species should be considered with caution, as only six species were measured. In addition, our experimental design

does not allow associations resulting from fundamental constraints to be disentangled from those arising from indirect relationships through third variables (in our case driven by changing water availability), which should constitute a priority for future research.

## Conclusion

Our study shows that plant adjustment along a water availability gradient involves many different suites of traits, and highlights the importance of ITV for understanding the capacity of plants to buffer against environmental changes. The availability of individual/plot-level trait data coupled with environmental and site information will allow more accurate model parameterization and, therefore, better predictions of species' responses to global change (Moran *et al.*, 2016). We show that, within species, plant adjustments along a water availability gradient rely more on changes in allocation (Hv) and leaf tolerance to low water potentials ( $P_{\text{dp}}$ ) than on changes in xylem safety or efficiency. Finally, we show that the use of trait networks could accommodate the intricate, multivariate relationships shaping plant strategies to a much greater degree than approaches based on bivariate relationships (Poorter *et al.*, 2014; Messier *et al.*, 2017). Scale-dependent trait covariation networks can provide powerful insights when assessing the architecture of plant plasticity and its limits under changing environmental conditions.







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## Author contributions

JM-V, MM and TR planned and designed the research; TR and JB performed the measurements with contributions from HC, MM and JM-V; TR analysed the data; and TR wrote the first draft with contributions from JM-V, MM, SS-M, JB and HC.

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## Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

**Fig. S1** Map of study area showing the distribution of sampling plots along the water availability gradient.

**Fig. S2** Distribution of the precipitation to potential evapotranspiration ratio (P : PET) plot values for each sampled species.

**Fig. S3** Principal component analysis (PCA) conducted to summarize environmental variables at the plot level (climate, forest structure and soil characteristics).

**Fig. S4** Distribution of each trait as a function of species and family.

**Fig. S5** Variance partitioning within Pinaceae and Fagaceae families.

**Table S1** Characterization of the dominant species in the study plots.

**Table S2** Statistical descriptors of studied traits.

**Table S3** Results of the linear mixed models examining the relationships between environmental variables using the PCA axis and traits.

**Table S4** Results of the linear mixed models examining the effect of precipitation to potential evapotranspiration ratio (P : PET) on each trait within and among species.

**Table S5** Descriptors of trait networks across species and for each studied species separately.

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